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Potential Impacts of Bison Wallows on a Restored Tallgrass Prairie Community

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ABSTRACT When bison (*Bos bison*) repeatedly roll on the ground, they denude vegetation and create wallows (semi-permanent bare areas) that alter the native prairie plant community. Responses to these wallow-related disturbances are not as well documented in restored prairies. From 1 June to 1 September 2010 and from 3 June to 6 August 2011, we examined potential responses at Neal Smith National Wildlife Refuge, a restored prairie with resident bison. We hypothesized that plants and beetles would vary along a disturbance gradient. Our predictions were: (1) near wallows, plants with weedy lifestyles would have highest cover and biomass compared to plants with nonweedy lifestyles, (2) in control areas (i.e., nonwallows), weedy compared to nonweedy plant cover and biomass would not change over distance (measured from nonwallow locations with similar dimensions as their paired wallows), and (3) ground beetle abundance would increase further from wallows, but not change across distance at nonwallows. Results were varied. Indices of weedy to nonweedy plant cover and weedy to nonweedy biomass were highest adjacent to wallows, with no distance effect at nonwallows. Beetle abundance was affected by location but not distance, with more beetles trapped at nonwallows than wallows. Additionally, of the five common beetle genera, three were unequally distributed between wallows and nonwallows. Both plants and insects varied across wallows and nonwallows, but their responses along disturbance gradients likely occur at different scales.

KEY WORDS annual net primary productivity, ANPP, beetles, bison, *Bos bison*, cover, plants, prairie, wallow, weedy

Bison (*Bos bison*) are large herbivores that impact their native grassland communities via disturbance behaviors including grazing and wallowing (Hobbs and Huenneke 1992, Knapp et al. 1999, McMillan 1999, Martin et al. 2005). Grazing reduces biomass of frequently-consumed plants compared to less frequently-consumed plants (Hartnett et al. 1996, Towne et al. 2005). Wallowing removes all plant biomass from an area when bison roll back and forth on the ground and create a shallow bare depression (i.e., wallow; Gerlanc and Kaufman 2003).

A disturbance gradient for plants is associated with wallows. For example, wallows at Konza Prairie in Kansas contained higher plant cover percentages of grass species and annual species compared to areas 10 m away (Gibson 1989). Also at Konza, higher plant cover percentages of annual species and exotic species were detected at wallow edges compared to areas 5 m away (Trager et al. 2004). Additionally, when bison were excluded from wallows and adjacent regions for 2 years, annual net primary productivity (ANPP) at wallow edges was twice that of adjacent regions (approximately 2 m away, McMillan et al. 2011).

Plants with high tolerances for disturbance should be more common close to wallows than plants with low tolerances. Tolerant plants include those with "weedy" lifestyles such as annuals and biennials with fast growth rates (e.g., *Ambrosia artemisiifolia* and *Daucus carota*; Bazzaz 1974, Clark and Wilson 2003), and perennials that dominate their local environments (e.g., *Poa pratensis* and *Bromus inermis*; Trager et al. 2004, Vinton and Goergen 2006). Many native tallgrass prairie species are weedy if given the opportunity to become established, including the annual *A. artemisiifolia* and perennial *Ratibida pinnata* (Curtis 1959, Christiansen and Müller 1999). Plants with low tolerance for disturbance include those with "nonweedy" lifestyles that do not become dominant species in disturbed environments. Examples of nonweedy plants include many legumes, *Liatris* spp., and *Sporobolus heterolepis* (Curtis 1959, see Ritchie and Tilman 1995 for additional examples).

Insects are also affected by disturbances (e.g., vegetation removal). Dragonflies and damselflies used wallows as temporary ponds to complete their metamorphoses (Jewell 1927, Voshell 2002). Abundances of the most commonly trapped ground beetle species (carabids) varied with mowed or bare ground and patch size of bare ground in heathland habitat (Cameron and Leather 2012). Decreases in structural heterogeneity of wetland plants via vegetation removal negatively impacted the activity-abundances of large Carabid species (Brose 2003). Ground beetle species assemblages may be considered indicators of habitat type (e.g., prairie) and potential environmental alterations in those habitats (Larsen et al. 2003).

Like plants, a disturbance gradient associated with wallows may exist for insects. Carabid species assemblages located in high disturbance agricultural areas differed from those detected in less disturbed prairies (Larsen et al. 2003). Also, ground beetle abundance and species numbers decreased in response to more intense plowing methods associated with conventional tillage compared to less intense weed

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cultivation (Kromp 1999), and abundance increased with time since last cultivation disturbance in fields of five different crops (Ward et al. 2011). Additionally, carabid abundances were inversely correlated with trampling frequencies in urban environments (Grandchamp et al. 2000).

Due to the documented impacts of bison wallows within native prairies, we hypothesized that wallows would impact the plant and ground beetle community in a restored tallgrass prairie, along a disturbance gradient. Our three predictions were: (1) weedy compared to nonweedy plant cover and biomass would be highest at wallows and then decrease further from wallows, (2) in control areas (i.e., nonwallows), weedy compared to nonweedy plant cover and biomass would not change over distance (measured from nonwallow locations with similar dimensions as their paired wallows), and (3) ground beetle abundance would increase further from wallows, but not across distance at nonwallows.

STUDY AREA

Neal Smith National Wildlife Refuge (NSNWR, 41° 33´N, 93° 17´W) near Prairie City, Jasper County, Iowa, represents one of the largest tallgrass prairie restorations (2,266 ha) in North America (Fig. 1; Friends of Neal Smith National Wildlife Refuge [FNSNWR] 2008*a*). In the 1990s, refuge managers began restoration at NSNWR and introduced bison to a 283 ha enclosure (FNSNWR 2008*b*). Dominant species at NSNWR include native and exotic grasses *Andropogon gerardii*, *Sorghastrum nutans*, and *Poa pratensis*, and forbs such as *Helianthus grosseserratus* (Martin et al. 2005). Our field seasons extended from 1 June to 1 September 2010 and from 3 June to 6 August 2011. Mean county temperatures and precipitation levels for June–August 2010 were 23.5° C and 26.8 cm and for June–August 2011 were 23.8° C and 10.5 cm (Iowaagriculture 2013).

METHODS

Plant and Insect Transects

In June 2010, we randomly selected seven "active" wallows using a predetermined set of characteristics and then mapped the Global Positioning System (GPS) coordinate for the zero south (0 S) edge of each wallow using a Garmin® GPSMAP 60CSx™ (± 3 m accuracy; Garmin International Inc., Olathe, KS; Fig. 2). Each wallow was located >50 m from each other and >20 m from wallows not studied, there were no more than two annual seedlings and no perennials inside each wallow, and each location was within an elevation range of 260–280 m on the Tama silty clay loam soil series (U.S. Department of Agriculture [USDA] 1979).

After recording 0 S, we determined the zero north (0 N) point by laying a meter tape in a due N–S direction (using a compass) and connecting the north and south edges of the wallow. We recorded the distance (N–S diameter) along with the 0 N GPS coordinate. We measured the E–W diameter using the same method after finding 0 E at 90° to the N–S axis. We placed temporary flagging at each of the four compass points to assist with diameter measurements, but removed the flagging before moving on to the next wallow to prevent any interactions between bison and flagging.

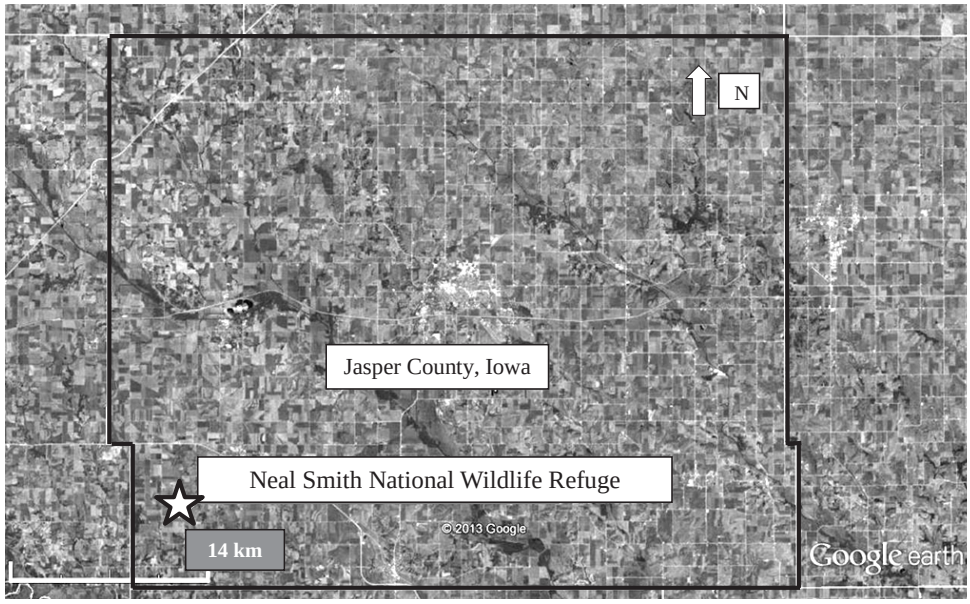

Figure 1. Location of Neal Smith National Wildlife Refuge (star shape) in the Southwest corner of Jasper County (bold outline), Iowa (image credit: Google Earth 2013).

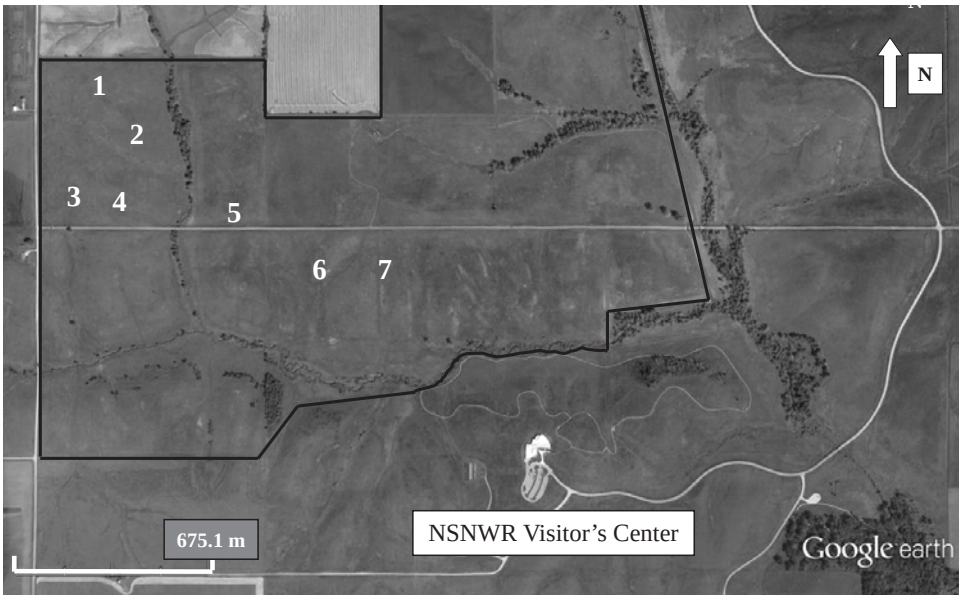

Figure 2. Aerial photo of seven wallow locations within the bison enclosure (bold outline) at Neal Smith National Wildlife Refuge (NSNWR), Iowa. The horizontal solid line is 96th Avenue running east-west through the bison enclosure. The NSNWR Visitor's Center is located south of 96th Avenue. Corresponding nonwallows located 25 m N or S of the wallows were not included in this photo.

We paired each wallow with a control (i.e., nonwallow) located 25 m N or S (Fig. 3) and minimized errors from field variation, using slope, management history (e.g., burn frequencies and mowing), and elevation. Final decisions on nonwallow placements depended on avoiding active wallows within 25 m of the nonwallows, a road, or fence. Each nonwallow was a region of prairie with the same dimensions (N–S and E–W diameters) as the corresponding wallow. We mapped and marked 0 N, 0 S, 0 E, and 0 W using GPS, compasses, meter tapes, and temporary flagging.

Following mapping of wallow and nonwallow pairs, we used GPS coordinates, compasses, and meter tapes to create transects to measure potential distance effects. We measured and flagged 4 E, 8 E, 4 S, and 8 S for wallows and nonwallows (Fig. 3). For wallow 5, we did not collect plant data or invertebrates at 4 S or 8 S due to the presence of the public road that bisected the enclosure (Fig. 2). During the 2011 field season, we reestablished all points using GPS coordinates, compasses, and meter tapes. We measured and flagged 8W for wallows and nonwallows.

Plant Cover and Biomass

We collected plant cover data during 2 July–1 September 2010 and 25 July–3 August 2011. Our data collection efforts differed between years due to variation in field assistance. We placed a hula hoop (area: 0.61 m^2) at 0, 4, and 8 m along the S and E transects at wallows and corresponding nonwallows (Fig. 3). We identified plants to genus or species (when possible) using several sources (Brown 1979, North Central Regional Technical Committee 1981, Barkley 1983, Christiansen and Müller 1999, USDA 2012). We assessed plant cover and bare ground using a modified Daubenmire scale (Trager et al. 2004, Foster 2006). Instead of using cover classes with uneven amounts of cover (e.g., 'Daubenmire' class 5: 75 $\leq$ x < 95% cover, class 6: $\geq$ 95% cover, Daubenmire 1968), we used plant classes with equivalent cover to improve accuracy of data collection and to ensure evenly spaced midpoints within each percent cover class. Our plant cover classes were assigned as follows: 1 (1–17%), 2 (17–34%), 3 (34–51%), 4 (51–68%), 5 (68–85%), 6 (85–100%). We assigned "trace" to any genus or species that had <1% cover.

On 25–27 July, 29 July, and 1–3 August in 2011, we collected biomass for wallows and nonwallows by clipping plants to ground level using 0.25 m^2 plots at 0 W and 8 W (Fig. 3). Due to limited field assistance, we did not collect biomass data during 2010. To reduce influencing plant cover and insects, we avoided E and S transects. Using taxonomy consistent with the plant cover data, we identified all biomass and stored it in paper bags labeled with location and distance. At Wartburg College, we dried samples in a Quincy Lab GC 40 drying oven (Quincy Lab, Inc., Chicago, IL) at 80° C for 24 hr (Pooter and Remkes 1990) and weighed plants inside their bags, to the nearest tenth of a gram using a top loading balance (Fisher Scientific, Pittsburgh, PA). We calculated ANPP (i.e., plant biomass) as the difference between the dried bag mass before and after plant removal. We classified plant species or genera that consisted of <1 g as "trace."

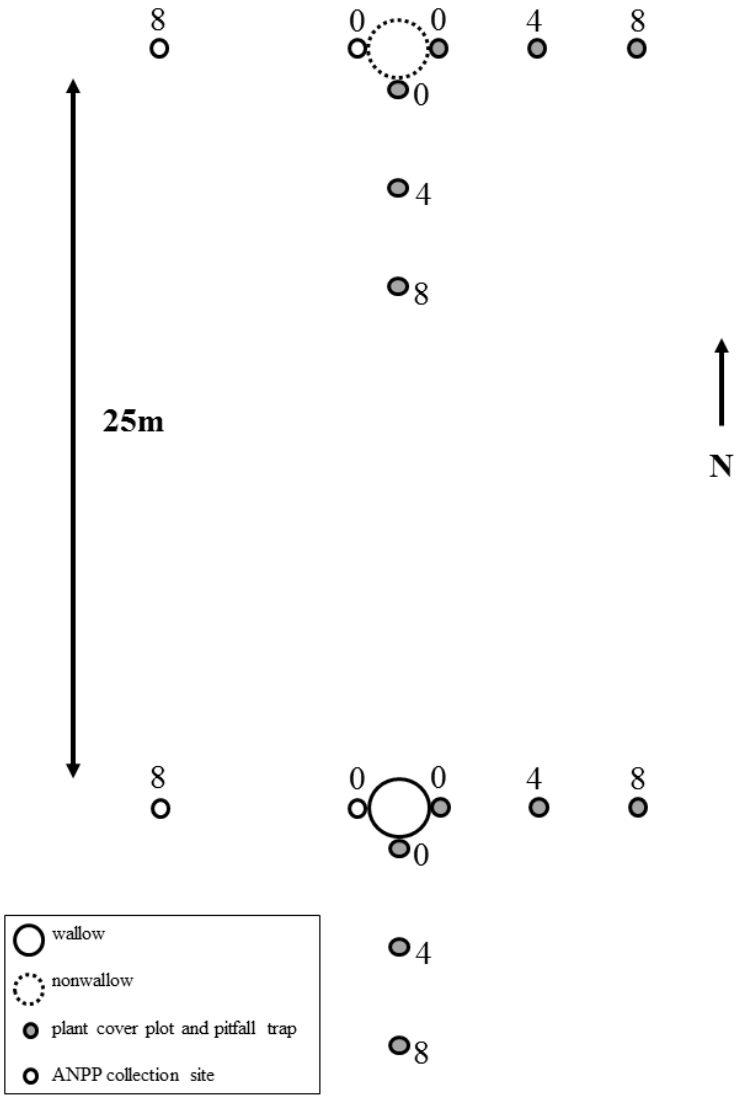

Figure 3. Schematic diagram of wallow and nonwallow pairs investigated at Neal Smith National Wildlife Refuge, Iowa, summer 2010 and 2011. Large circles represent wallows (solid line) and nonwallows (dashed line). Small white circles represent annual net primary productivity (ANPP) collection sites. Small gray circles represent plant cover plots and pitfall traps, all spaced at 0, 4, or 8 m from the edge of a wallow or nonwallow.

Following data collection, we grouped plants as weedy or nonweedy. Weedy plants included those species documented as tolerant of high disturbances, regardless of whether they were annuals, biennials, or perennials (Curtis 1959, Christiansen and Müller 1999, Ladd and Oberle 2005, USDA 2012). Nonweedy plants included those species documented as intolerant of high disturbances, or specifically not listed as weedy (Curtis 1959, Christiansen and Müller 1999, USDA 2012).

Ground Beetle Abundance

In 2011 (8 June, 5–6 July, and 3–4 August), we collected ground beetles using pitfall traps (Lövei and Sunderland 1996). We always collected pitfall traps prior to collecting plant cover data and biomass. In both July and August, we set half of the traps on the first day and the other half on the second day. To reduce collection bias, we reversed the set-up order in August.

We placed pitfall traps (i.e., plastic cups, 9-cm diameter, 15-cm depth) flush with the ground and added 75 mL of the preservative 70% isopropyl alcohol. We placed traps along the existing E and S transects, at 0, 4, and 8 m, for each of the 6 wallow/nonwallow pairs (72 traps total; Fig. 3). We did not place traps at wallow 2 due to time constraints associated with digging 72 holes in hard soil. We collected insects from traps on the third day. We removed all traps on the collection dates to reduce impact on bison. We stored all specimens

at Wartburg College and identified beetles to genus (Triplehorn and Johnson 2005, Eaton and Kaufman 2007, BugGuide 2012).

Statistical Analyses

Plant cover and biomass.—We converted plant cover class data into median percent cover for each species or genus by identifying the midpoint percent for each of the aforementioned cover classes (e.g., 0 and trace = 0, 1 = 9%, 2 = 25.5%, 3 = 42.5%, 4 = 59.5%, 5 = 76.5%, 6 = 92.5%, *sensu* Gibson 1989, Trager et al. 2004). For each distance (0 E, 4 E, 8 E, 0 S, 4 S, and 8 S) at each wallow and nonwallow, we summed the median percent cover of weedy plants and did the same for median percent cover of nonweedy plants. We used GraphPad InStat version 3.00 for Windows (GraphPad Software, San Diego, CA) to run Wilcoxon signed-rank tests to determine if E and S weedy percent cover sums could be pooled (i.e., averaged) at each distance (e.g., 0 E and 0 S) across wallows, and across nonwallows. We did the same for nonweedy percent cover sums. If similar, we pooled E and S weedy percent cover sums at each distance (e.g., 0 E and 0 S, 4 E and 4 S, 8 E and 8 S) for each wallow, and nonwallow, and likewise for nonweedy percent cover sums. If different, we did not pool E and S data.

For each distance (e.g., 0 E/S pooled, 4 E/S pooled, 8 E/S pooled), at each wallow, and nonwallow, we calculated an index of weedy to nonweedy plant percent cover (WNCI) by dividing the percent cover sum for weedy plants by the percent cover sum for nonweedy plants. Because this index could not be transformed to obtain normally distributed data, we used nonparametric statistical tests. First, we used Wilcoxon signed-rank tests to determine if 2010 and 2011 WNCI could be pooled (i.e., averaged) at each distance for wallows, and for nonwallows. If similar, we pooled 2010 and 2011 indices at each distance, for each wallow, and nonwallow. We used Friedman's tests with Dunn's multiple comparisons to compare WNCI across the three distances for wallows, and for nonwallows. We analyzed ANPP data similarly. However, we did not compare data across E and S transects or across years, because our ANPP data existed only for W transects in 2011. Also, because we assessed ANPP at two distances (i.e., 0 and 8 m), we used Wilcoxon signed-rank tests to compare the index of weedy to nonweedy ANPP (WNAI) across distance for wallows, and for nonwallows.

Ground beetle abundance.—During the June collection, we successfully established only two sets of pitfall traps. Therefore, our statistical analyses focused on July and August 2011 data. Within genera, we summed beetles trapped in July and August. We used Wilcoxon signed-rank tests to determine if E and S transect data could be pooled for each distance for wallows, and for nonwallows. If similar, we averaged beetle numbers at each distance for each wallow, and each nonwallow.

We used PRIMER 6 (version 6.1.13) with PERMANOVA + (version 1.0.3; PRIMER-E Ltd., Plymouth PL1 3DH, UK) software to run a permutational multivariate analysis of variance (PERMANOVA) to test effects of distance and location on beetle abundance across beetle genera (*sensu* Gibb et al. 2006), if the sum of their percent representation at wallows and nonwallows was ≥5% (Table 1). This permutational analysis does not require the assumptions of normality and homogeneity of variances to be met. The model included a random factor: block (wallow or nonwallow ID number) and two fixed factors: location (wallow or nonwallow) and distance (0, 4, 8 m). We transformed beetle abundance using the fourth root to decrease the influence of a dominant genus and provide a more accurate representation of how multiple genera varied across the prairie community (Gibb et al. 2006). We used the Bray-Curtis similarity (+d) index to assess the resemblance matrix created from 9,999 permutations (Gibb et al. 2006). We sequentially removed interaction terms with negative components of variation (i.e., not significant) from the model and we pooled their components of variation and degrees of freedom with residuals, allowing for greater statistical power for the terms left in the model (*sensu* Harding et al. 2011).

RESULTS

All wallows were approximately circular, averaged 7.3 m^2 (SE = 0.5), and remained active throughout the study. Average N–S axes and E–W axes were equivalent ($\bar{x}$ = 3.2 m^2, SE = 0.2, n = 7; $\bar{x}$ = 3.2 m^2, SE = 0.2, n = 7).

Plant Cover and Biomass

In 2010, we identified 47 plant species (or genera) on plant cover transects: 24 weedy and 23 nonweedy (2 of the weedy species were "trace"; Appendix 1). In 2011, we identified 45 plant species (or genera) on plant cover transects: 24 weedy and 21 nonweedy (3 of the weedy species and 1 of the nonweedy species were "trace"; Appendix 1). In 2011, we identified 36 species (or genera) on biomass transects: 20 weedy and 16 nonweedy (3 of the weedy species and 4 of the nonweedy species were "trace"; Appendix 1). For 2010 and 2011, E and S weedy percent cover sums were similar at each distance (e.g., 0 E and 0 S, 4 E and 4 S, 8 E and 8 S) for wallows, and for nonwallows ($P \geq 0.06$). The same was true for nonweedy percent cover sums ($P \geq 0.08$). Therefore, we averaged E and S weedy percent cover sums at each distance (e.g., 0 E/S pooled, 4 E/S pooled, 8 E/S pooled) for each wallow, and each nonwallow in 2010 and 2011. We did the same for E and S nonweedy percent cover sums. Also, no differences were detected between 2010 and 2011 WNCI at any distance for wallows or nonwallows ($P \geq 0.11$). Therefore, we pooled indices across years for each distance, at each wallow, and nonwallow. The WNCI varied across distance for

Table 1. Beetle genera, total numbers of individuals detected at wallows and nonwallows, and genus representation in collection of beetles trapped at Neal Smith National Wildlife Refuge, Iowa, July–August 2011.

Beetle genera	Total individuals (# at wallows, # at nonwallows)	Percent of entire collection	Percent at wallows, within genus[a]	Percent at nonwallows, within genus[a]	Percent representation at wallows, across genera[b]	Percent representation at nonwallows, across genera[b]
Acupalpus	2 (0, 2)	0.01	0.00	1.00	0.00	0.01
Carabus	7 (4, 3)	0.02	0.57	0.43	0.03	0.01
Chlaenius	38 (24, 14)	0.11	0.63	0.37	0.20*	0.07
Cicindela	2 (1, 1)	0.01	0.50	0.50	0.01	0.00
Cyclotrachelus	127 (33, 94)	0.38	0.26	0.74	0.27	0.45*
Galerita	23 (2, 21)	0.07	0.09	0.91	0.02	0.10*
Lachnocrepis	5 (3, 2)	0.01	0.60	0.40	0.02	0.01
Loxandrus	80 (24, 56)	0.24	0.30	0.70	0.20	0.27*
Poecilus	1 (1, 0)	0.00	1.00	0.00	0.01	0.00
Pterostichus	49 (31, 18)	0.15	0.63	0.37	0.25*	0.09
Total	334 (123, 211)					

[a] Percent found at wallows (or nonwallows) was calculated by dividing the total number of beetles per genus at wallows (or nonwallows, respectively) by the total number of beetles per genus; [b] Percent representation at wallows (or nonwallows) across genera was calculated by dividing the total number of beetles for each genus at wallows by 123 (or the total number of beetles for each genus at nonwallows by 211, respectively). All genera with a percent total representation ≥5% were identified with '*' at their primary capture location.

wallows ($\chi^2_2 = 11.14$, $P = 0.001$, $n = 7$; Fig. 4), with post-tests indicating differences between 0 and 4 m ($P < 0.01$) and 0 and 8 m ($P < 0.05$). The average WNCI at 0 m was three times that of 4 m and 8 m at wallows (Fig. 4). The WNCI did not vary across distance for nonwallows ($\chi^2_2 = 0.00$, $P > 0.99$, $n = 7$; Fig. 4).

Relative to ANPP, the WNAI varied across distance for wallows ($T_2 = 28.0$, $P = 0.02$, $n = 7$; Fig. 5). The average WNAI at 0 m was two orders of magnitude greater than at 8 m at wallows. The WNAI did not vary across distance for nonwallows ($T_2 = 14.0$, $P > 0.99$, $n = 7$; Fig. 5).

Ground Beetle Abundance

During July and August, we collected 334 beetles, with 123 (37%) trapped at wallows and 211 (63%) trapped at nonwallows (Table 1). We identified ten Carabidae genera, with *Cyclotrachelus, Loxandrus, Pterostichus* and *Chlaenius* being the most common. Within genus, the average percent of individuals detected at wallows was 46%, while the average detected at nonwallows was 54% (calculated from date in Table 1). Across genera, the percent representation of beetles detected at wallows ranged between 0–27% and at nonwallows between 0–45%. At wallows, the most common genera included *Cyclotrachelus, Pterostichus and Chlaenius*, while the most common genera at nonwallows included *Cyclotrachelus* and *Loxandrus* (Table 1).

Beetle numbers at E and S transects for each distance at wallows and at nonwallows were similar ($P \geq 0.31$). Therefore, we averaged beetle numbers across E and S transects at each distance for wallows, and for nonwallows. The main effects block and location were significant in the PERMANOVA model (that included: *Chlaenius*, *Cyclotrachelus*, *Galerita*, *Loxandrus*, and *Pterostichus*; block: *pseudo*-$F_{5,20} = 7.48$, $P < 0.001$; location: *pseudo*-$F_{1,5} = 4.62$, $P = 0.047$; Table 1), indicating the beetle community varied with specific locations of wallows and nonwallows and whether the location was a wallow or nonwallow. Distance and interactions between factors were not significant in the model ($P \geq 0.18$).

To further explore the impact of location on beetle community, we used a post-hoc chi-square test to compare the total number of individuals detected at wallows (123) and nonwallows (211) to expected numbers (334/2 = 167) generated if distribution was equal (Table 1). Observed and expected values differed ($\chi^2_1 = 23.2$, $P < 0.001$), indicating an unequal distribution of individuals at wallows compared to nonwallows.

In other post-hoc comparisons, we further assessed the five most common beetle genera (i.e., *Chlaenius*, *Cyclotrachelus*, *Galerita*, *Loxandrus*, and *Pterostichus*; Table 1). For

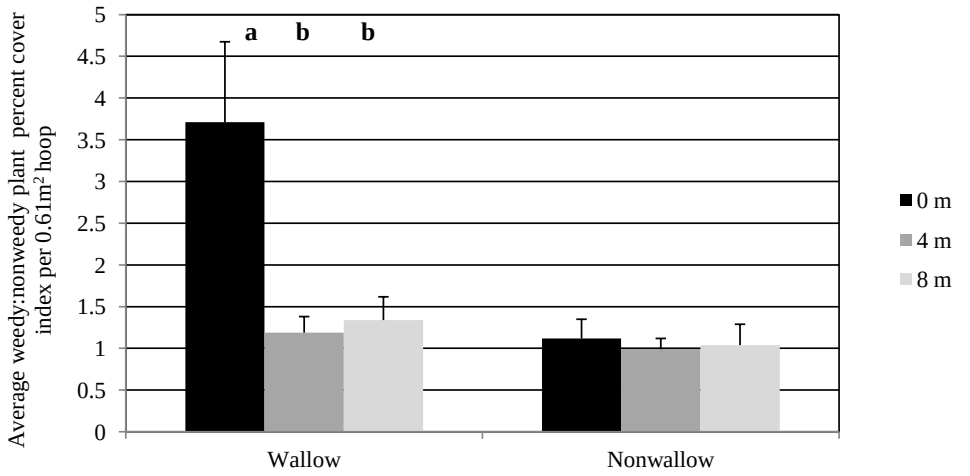

Figure 4. Average index (ratio) of weedy to nonweedy plant percent cover per hoop (0.61 m^2) at Neal Smith National Wildlife Refuge, Iowa. Indices were pooled across 2010 and 2011 and compared across 3 distances (0, 4, 8 m) for 7 wallows and nonwallows. Different letters indicate significant differences ($P < 0.05$) between distances at wallows or nonwallows. Standard error bars are shown.

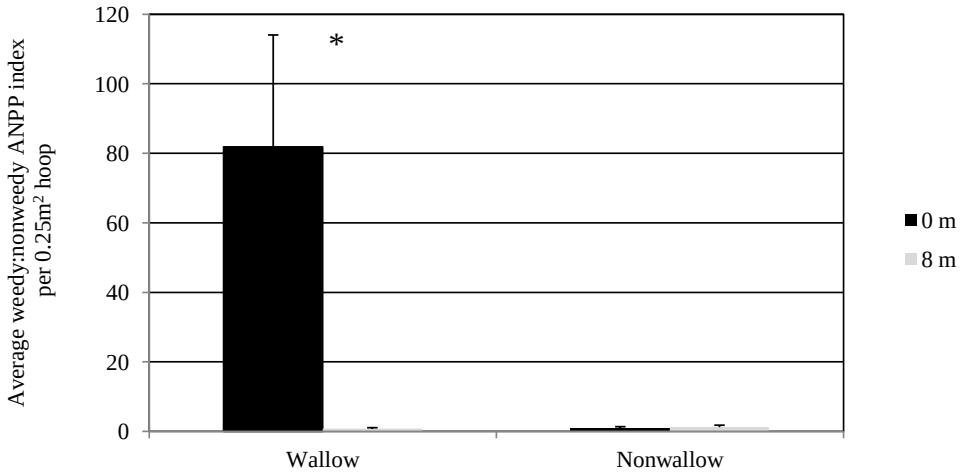

Figure 5. Average index (ratio) of weedy to nonweedy annual net primary productivity (ANPP) per hoop (0.25 m^2) at Neal Smith National Wildlife Refuge, Iowa. Indices from 2011 were compared across 2 distances (0 m, 8 m) at 7 wallows and nonwallows. An '*' indicates significant differences ($P < 0.05$) between distances at wallows or nonwallows. Standard error bars are shown.

each of these 5 genera, we classified the location where most beetles were trapped (either wallows or nonwallows) as the "primary capture location", using wallow and nonwallow totals for each genus (Table 1, Fig. 6). For each genus, we classified the location where fewer beetles were trapped as the "secondary capture location." For each genus, we performed a chi-square test to determine if the total abundance at primary locations and at secondary locations varied from expected values associated with equal distribution across the two locations. We calculated expected values for both primary and secondary locations as the total number of beetles trapped/2, for each genus. Three of the five most common genera were distributed unequally across primary and secondary locations (all three: $P < 0.001$): *Cyclotrachelus* ($\chi^2_1 = 29.3$), *Galerita* ($\chi^2_1 = 15.73$), and *Loxandrus* ($\chi^2_1 = 12.8$; Fig. 6). All three genera were trapped more often at nonwallows than wallows (Table 1, Fig. 6). *Chlaenius* and *Pterostichus* were trapped equally across primary and secondary locations.

DISCUSSION

Both predictions for plant cover were supported. Weedy plant cover was higher than nonweedy cover close to wallows, as indicated by the high average WNCI at 0 m (Fig.

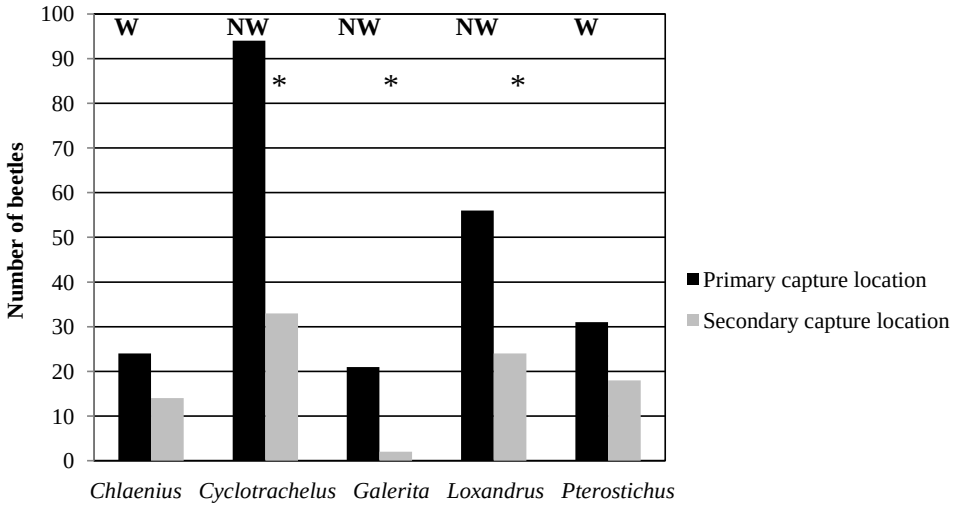

Figure 6. Beetle genera with ≥5% total representation among pitfall traps collected at Neal Smith National Wildlife Refuge, Iowa, summer 2011. For each genus, the location where most beetles were found (either wallows or nonwallows) was identified as the "primary capture location", using wallow and nonwallow totals for each genus, while the "secondary capture location" represented the location where fewer beetles were found. W (wallow) and NW (nonwallow) indicate the primary capture location for each genus. Within genera, observed and predicted numbers of beetles captured at primary and secondary capture locations were compared. For each genus, predicted values for both primary and secondary capture locations were generated assuming equal distribution across the two locations. An '*' indicates significant differences ($P < 0.05$) between observed and predicted values within genus, and therefore an unequal distribution across wallows and nonwallows.

4), while the average WNCI of ~1 at 4 and 8 m indicated that weedy cover was equivalent to nonweedy cover farther from wallows. Average WNCI of ~1 at all distances for nonwallows indicated no distance effects and equivalent weedy and nonweedy plant cover (Fig. 4). These results support the presence of a disturbance gradient, favoring weedy species near disturbance and resemble other studies that discovered higher plant cover for annual species at wallow edges compared to 5 or 10 m away (Gibson 1989, Trager et al. 2004).

Both predictions for ANPP also were supported. Weedy ANPP was higher than nonweedy ANPP close to wallows, as seen with the high average WNAI at 0 m (Fig. 5), while the average WNAI of <1 at 8 m indicated higher nonweedy than weedy ANPP at that wallow distance. Average WNAI of <1 at all distances for nonwallows indicated no distance effects and higher nonweedy than weedy ANPP. Indices of ANPP varied in concordance with plant cover at wallows. Likewise, other studies have documented higher ANPP at wallow edges compared to 2 m away (over 2 years of succession, excluding bison; McMillan et al. 2011). Disturbance, in the form of wallows, seems to act as an agent of selection in prairie microenvironments, favoring weedy species. As a result, wallow density and distribution are predicted to impact the patch mosaic of the prairie plant landscape and organisms at associated trophic levels.

The prediction that beetle abundance would be affected by distance at wallows was not supported. Potentially, beetles respond to disturbance at distances greater than 8 m because they are more mobile than plants. Alternatively, the beetle community was impacted by block and location. As we investigated individual genera and their possible adaptations to one location over another on a larger scale (wallows compared to nonwallows, separated by 25 m), we discovered that three of the five most common genera were more abundant in traps at nonwallows rather than wallows (Fig. 6). Additionally, although *Cyclotrachelus* (the most common genus in our traps) was the most common genus at wallows, their total number at nonwallows (primary capture location) was significantly higher than at wallows (secondary capture location, Fig. 6). Similarly, on a short-grass prairie in Colorado, *Cyclotrachelus* occurred least often in areas of higher disturbance and less vegetation (McIntyre 1998).

Our data support results of other studies indicating an inverse relationship between beetle abundance and disturbance (Kromp 1999, Grandchamp et al. 2000, Ward et al. 2011). Other than destruction of plants where wallows are created, disturbance could also occur in the form of bison movement towards and away from these focal points. As a result, due to their relative mobility (as compared to plants), some beetle genera could avoid areas near wallows. Thus, wallow density and distribution are predicted to influence abundance of ground beetles and associated trophic levels across the prairie landscape. Additionally, given the relatively even representation of the five common beetle genera collected in traps at

wallows, as compared to a dominant genus (*Cyclotrachelus*) collected in traps at nonwallows (Table 1, Fig. 6), habitat heterogeneity imposed by wallows may reduce the ability of certain genera to dominate areas surrounding wallows, thereby affecting the distribution of beetles in prairie habitat.

Our results highlighted how plants and insects vary in their scale of response to disturbance. The relative cover and biomass of weedy to nonweedy plants decreased between 0 and 8 m from wallows, while beetle abundance did not vary over this distance from wallows. However, given that beetle abundance varied between wallows and nonwallows, beetles might be responding to disturbance associated with wallows at the scale of ~30 m (25 m separating wallows and nonwallows + 8 m S transect distance; Fig. 3) from wallows.

MANAGEMENT IMPLICATIONS

While it is well documented that bison wallows have an impact on native prairies, the impacts of wallows on restored prairie are not well studied. However, given the paucity of restored prairies, understanding how disturbance from endemic animals and anthropogenic activities (e.g., historical farming practices) affect the prairie community is important. Future research should include collecting additional beetles and identifying them to species, because habitat distribution differences likely exist between conspecifics. Also, trapping beetles over longer distances at wallows and nonwallows could aid in identifying the possible disturbance gradient for beetles. Additionally, given the inverse relationship between ground beetle abundance and trampling frequencies in urban environments, quantifying the extent to which beetle abundance is impacted by bison trampling to and from wallows vs. nonwallows is warranted. We also recommend evaluating whether wallows act as "hotspots" that increase trampling frequencies as compared to areas lacking wallows. Because our data corroborate the contribution of wallows to patchy distributions of plants and beetles, we suggest that managers incorporate some form of controlled disturbance into prairie restoration and conservation efforts.

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Appendix 1. Plant genera and species recorded at Neal Smith National Wildlife Refuge, Iowa, 2010 and 2011.

Scientific name	PL[a]	2010 PC[b]	2011 PC[b]	2011 ANPP[c]
Achillea millefolium	NW		X	
Ambrosia artemisiifolia	W	X	X	X
Ambrosia trifida	W	X	X	X
Andropogon gerardii	NW	X	X	X
Apocynum cannabinum	W	X	X	
Asclepias syriaca	NW	X	X	
Bromus arvensis	W	X	X	X
Bromus inermis	W	X	X	X
Carex sp.	NW			X
Chamaecrista fasciculata	NW	X	X	X
Cirsium vulgare	W	X	X	X
Convolvulus arvensis	W	X	X	
Convolvulus sp.	W			tr
Conyza canadensis	W	X		
Daucus carota	W	X	X	X
Dichanthelium sp.	NW			tr
Digitaria ischaemum	W	X	X	X
Echinochloa crus-galli	W	X		X
Elymus canadensis	NW	X	X	X
Erigeron sp.	W		X	
Gaura sp.	NW	X		
Gentiana sp.	NW	X		
Helianthus grosseserratus	NW	X	X	X
Helianthus rigidus	NW	X		
Helianthus sp.	NW	X	X	X
Heliopsis helianthoides	NW	X		
Heuchera sp.	NW		X	tr
Hordeum pusillum	W			X
Lactuca sp.	W		X	tr
Lespedeza capitata	NW	X	X	X
Liatris sp.	NW	X	X	tr
Medicago lupulina	W	X	X	X
Melilotis sp.	W	X	X	X
Monarda fistulosa	NW	X	X	X
Oxalis stricta	W	tr		
Panicum virgatum	NW	X	X	
Phalaris arundinacea	W	tr	X	X
Phleum pratense	W	X		X
Physalis sp.	W	X	X	
Plantago sp.	W	X	X	
Poa pratensis	W	X	X	X
Pycnanthemum virginianum	NW	X		
Ratibida pinnata	W	X	X	
Rumex crispus	W	X		
Schizachyrium scoparium	NW	X	X	X
Silphium integrifolium	NW	X		
Solanum sp.	W		tr	
Solidago rigida	NW	X	X	
Solidago sp.	NW	X	X	X
Sorghastrum nutans	NW	X	X	X
Sporobolus heterolepis	NW			tr
Symphyotrichum sp.	NW	X	X	X
Taraxacum officinale	W	X	X	X
Teucrium sp.	NW		X	
Thlaspi arvense	W		tr	tr
Trifolium pratense	W	X	X	X
Trifolium repens	W	X	X	X
Ulmus sp.	NW		tr	
Verbena sp.	NW	X	X	
Xanthium sp.	W		tr	
Zizia aurea	NW	X	X	

[a] PL indicates plant lifestyle and includes W (weedy) and NW (nonweedy); [b] PC indicates plant identified during cover data collection. PC transects included 0, 4, and 8 m East and South. Plants labeled "tr" (trace) had <1% cover; [c] ANPP (annual net primary productivity) indicates plant identified during biomass collection. ANPP transects included 0 and 8 m West. Plants labeled "tr" (trace) consisted of <1 g.